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ABSTRACT

This is the first report of ultraviolet-absorbing corolla veins in the genus Jaltomata, and the first report of ultraviolet-absorbing nectar for the Solanaceae. The corolla of the species studied, J. weigendiana, is green and campanulate and reflects light in the ultraviolet (UV) part of the spectrum. The UV-absorbing radial corolla veins are hypothesized to serve as nectar guides. Five radial staminal-corolla thickenings create nectar troughs between the radial thickenings. The nectar is visibly red and, like the corolla veins, strongly absorbs UV radiation. Nectar volume from greenhouse-grown plants ranged from 7 to 57 µl (mean 28) and estimates of sugar concentration ranged from 9 to 24 % (mean 15). J. weigendiana is a new species, distinguished from congeners by having no more than two flowers per inflorescence and by lacking both a corolla limb and corolla lobules. Fruits of this species are eaten by local people. Published on-line www.phytologia.org Phytologia 100(1): 12-18 (Mar 16, 2018). ISSN 030319430.

KEY WORDS: colored nectar, edible fruit, foraging signal, Huánuco, nectar guide, Peru, protogyny, red nectar, UV absorptive nectar.

The genus Jaltomata includes about 70 diverse species, growing from Arizona, USA, to Bolivia, on the Galápagos Islands and in the Greater Antilles (Mione et al., 2015). Here we describe a new species having red floral nectar. The Jaltomata species having red floral nectar grow in the Andes of South America (Mione & Anderson, 1996; Hansen et al., 2007; Leiva González et al., 2015), and the new species we describe is from Department Huánuco, Peru. We collected this species during fieldwork in 2016.

MATERIALS AND METHODS

Plants were grown at Central Connecticut State University from seeds collected with the type collection. Ultraviolet photos were taken with a Canon EOS Rebel T5i camera having a Full Spectrum Conversion (<u>www.lifepixel.com</u>). To prevent visible and infrared light from entering the camera a StraightEdgeU (www.uvroptics.com) bandpass filter was used (on a Canon EF 50 mm f/1.8 lens with a Hoya +4 close-up). Flowers were illuminated with a UVP UVL-56 hand-held lamp. A UV-Visible Spectrophotometer (Evolution 201) was used to measure absorbance (3 µl of nectar were diluted to 20 ml in deionized water). Nectar volume was measured with microcapillary tubes and sugar concentration was

estimated with a refractometer. Six flowers of unknown age (fully open but not senescing) were used; nectar had not been removed previously.

Stalked glands have multicellular heads and unicellular stalks, the heads staining densely with neutral red (as illustrated in Mione & Serazo, 1999). The other hairs lack multicellular heads: dendritic hairs are uniseriate and many-celled with three or more branches emerging at different levels; forked hairs are also uniseriate and many-celled but have only two termini; finger hairs are uniseriate and unbranched. In the following description, unless indicated otherwise, hairs are not gland-tipped and are unpigmented. Pollen size is based on 28 grains in polar view stained with cotton blue in lactoglycerol. The reported seed counts and fruit size are from two field-collected fruits. Species authorities are provided in Appendix 1.

Jaltomata weigendiana Mione & S. Leiva sp. nov. Type: Peru. Dept. Huánuco: Prov. Huamalíes, 3,727 m, 9 24' 54" S, 76 45' 24.6" W, rock wall between agricultural fields, 21 & 22 May 2016, T. Mione, S. Leiva G. & L. Yacher 873 (F). (Figures 1 & 2).

Inflorescence 1–2 flowered, corolla campanulate and green, lacking a corona, corolla limb and corolla lobules, radial staminal-corolla thickenings (five) creating nectar troughs (five) between the radial thickenings, the stigma capitate.



Figure 1. Protogyny of Jaltomata weigendiana. A. Pistillate phase (anthers undehisced). B. Hermaphroditic phase (anthers dehisced). Scale bars represent 1 cm. A. Cultivated plant, in sunlight, by Sara K. Popolizio. **B**. At the site of the type collection, with a flash, by T. M.

Shrub 1–1.5 m high, the young branches green, pubescent with erect, finger, forked and dendritic hairs, sometimes gland tipped, the older stems brown, glabrous, with lenticels (Figure 2E), terete, and to 1.2 cm diameter. Leaves alternate or geminate, the blade to 10 cm long \times 5.6 cm wide but commonly smaller, darker green above, ovate to elliptical-lanceolate, the apex acute (Figure 2C), both faces densely pubescent with finger, forked and dendritic hairs; petiole to 2.2 cm long. Inflorescence 1–2 flowered; peduncle 4–7 mm long, green at flowering, terete, pubescent with erect, finger, forked and dendritic hairs; pedicel 10-11 mm long, green at flowering, terete, pubescent with erect, finger, forked and dendritic hairs. Calyx green, 15-20 mm diameter, the lobes weakly recurved (Figures 1B, 2A), adaxially with a dense covering of stalked glands (that have multicellular heads) 0.06 mm long, abaxially pubescent with dendritic, forked and finger hairs; the calyx 23.5–30 mm diameter at fruit maturity (Figure 2D). Corolla green, with radial UV absorbing veins (Figure 2A), campanulate, 8–10 long × 25–30 mm diameter, 5-lobed and lacking lobules (Figure 1), externally pubescent the hairs 0.2 to 0.25 mm long, mostly fingerlike, but some forked and a few dendritic, internally puberulent with gland-tipped finger hairs 0.1–0.3 mm long; the nectar showing through the wall of the corolla. Stamens 9–10.5 mm long, exserted 3 mm beyond distal end of corolla; the radially oriented staminal-corolla thickenings create troughs between the radial thickenings, with copious red nectar pooling in troughs (Figure 1); the base of the filament expanded laterally (ventral view), the filaments connivent prior to anther dehiscence (Figure 1A), angling outward after anther dehiscence (Figure 1B); pale-green to off-white, pilose along 24–33% of the length proximally, with unpigmented finger hairs; the anther yellow (Figure 1A) with a green connective prior to dehiscence, 1.7 (dehisced)–2.8 (undehisced) long × 1.7 mm wide (fresh), not mucronate; mean pollen grain diameter 34 μ m. Stigma capitate, 0.8–0.85 × 0.95–1.05 mm, with a shallow medial groove, darker green than the style (Figure 1); style 8.2–8.5 mm long, straight, pale-green, exserted a few mm beyond distal end of corolla; ovary green, 2.8 high × 2.6 mm wide, the nectary disk orange and half as high as the ovary. Fruit orange (Figure 2B,C), 1.5 × 2 cm; 332–362 seeds per fruit.



Figure 2. Jaltomata weigendiana. **A**. Two photos of the same flower joined together: UV only on left, smaller arrows–UV absorptive nectar guide, larger arrow–nectar; visible light on right; units are mm. **B**. Fruits, orange when ripe; units are mm. **C**. Leaves and a ripe fruit, lower right leaf is lower face up; units along left are mm. **D**. Calyx from ripe fruit, one lobe missing due to herbivore damage; segment of ruler = 5 mm. **E**. Older branch with lenticels; units are mm. All photos were taken at the site of the type collection except **A**. was a cultivated plant; all photos were taken by T. M.

Additional specimens examined. PERU. Huánuco: Prov. Huamalíes, 9° 26' S, 76° 46' W, above Chavin De Pariarca, hedges between fields, 3600 m, 19 Mar 2001, *M. Weigend, K. Weigend, M. Binder & E. Rodriguez 5246* (Ref 2001/246, 6) (M); 3,727 m, 9 24' 54 S, 76 45' 24.6" W, rock wall between agricultural fields, 21/ 22 May 2016, *S. Leiva G. et al.* 6065 (HAO), *Mione et al.* 874 (CCSU).

	J. weigendiana	J. herrerae	J. estilopilosa	J. paneroi	J. neei	J. alviteziana	J. dendroidea	J. leivae
Country, Primary Political	Peru, Huánuco	Peru, Cuzco, Apurimac, Ayacucho. Bolivia, La Paz	Peru, Amazonas	Peru, Cajamarca	Peru, Cajamarca	Peru, Cajamarca	Peru, La Libertad	Peru, Cajamarca
Altitude (m)	3,600-3,727	3000 – 3750	2994	3240 – 3500	2400 - 2919	2960-3084	3100 – 3360	2560-2650
Leaf blade	pubescent	pubescent	pubescent	pubescent	pubescent	pubescent	pubescent	glabrate
Flowers Per Inflorescence	1–2	2–6	24	3–6	1–5	2–3	1-4	1–3
Calyx Diameter, flowering (mm)	14–19	21–26	11–15	13	16–18	13–20	17–21	15
Calyx Lobes	as long as wide	longer than wide	as long as wide	as long as wide	as long as wide	as long as wide	as long as wide	as long as wide
Calyx reflexed during anthesis	weakly	strongly	weakly	no	no	weakly to strongly	no to weakly	strongly
Calyx diameter, ripe fruit (mm)	30	40	20	25	25	20–28	23–25	26
Corolla color	green	green	green	pale-green	green turning blue	purple-blue	green	purple-blue
Purple pigment in base of corolla	no	yes	no data	yes	yes	yes	yes	yes
Corolla shape	campanulate	campanulate	tubular- campanulate	tubular- campanul ate	tubular- campanul ate	tubular- campanulate	tubular- campanulate	tubular- campanulat e
Corolla Limb	no	yes	yes	yes	yes	yes	yes	yes
Corolla lobes / lobules	5/0	5/5	5/5	5/5	5/5	5/5	5 / 5*	5/5
Corolla	25 20	20 40	24.25	20.25	25 20	25.27	22 20	14
Corolla Length (mm)	8-10	10-15	10-11	5-10	9–13	8-12	10-13	7-9
Percent of length of filament	24–33	3–5	3–5	3–15	5-10	2–3	to 23	20–25

Table I. Comparison of Jaltomata weigendiana with similar congeneric species.

mament	24-33	5-5	5-5	5-15	5-10	2-5	10 25	20 25
pubescent,								
proximal to								
distal								
Style length	8.2-8.5	14	11–11.5	7–11	11-13	7-10.2	12-12.5	9–18

* The corolla lobules of *J. dendroidea* were absent on one collection (*Mione et al.* 722) in the wild, but were present at the type collection and were present on flowers of plants of *Mione et al.* 719 grown by Jamie Kostyun.

Jaltomata weigendiana grows in Peru, Department Huánuco, province Huamalíes, between 3,600 and 3,727 m in the vegetation between agricultural fields. No other species of the genus *Jaltomata* has only one to two flowers per inflorescence, red nectar, and lacks a corona, a corolla limb and corolla lobules. Table 1 compares *J. weigendiana* with similar congeneric species: shrubs having a campanulate, tubular-campanulate or tubular-urceolate corolla, copious red/orange nectar, radial staminal-corolla thickenings creating five nectar troughs (one trough between each pair of thickenings), no corona, stamens connivent prior to anther dehiscence, yellow anthers but with a green connective on the dorsal face, and a capitate stigma. The corolla of *J. dendroidea*, *J. paneroi and J. weigendiana* remain open at night, and the corolla of other species in Table 1 have not been studied but almost certainly remain open at night given their similar corolla form.

We estimated the population size to be less than 1000 mature individuals, and thus using criterion D1 of the IUCN (2017) *J. weigendiana* is considered vulnerable (VU). Collections of this species were not present among the specimens borrowed from various herbaria, and thus it seems that the only place where it has been collected is the type locality. From discussion with two adults who live near the type locality we learned that the ripe berries are eaten by locals, "se comen," and the local name of this species is "antaraura." The name of this species was chosen to honor Dr. Maximilian Weigend who was the first to collect this species.

Flowers of *J. weigendiana* are protogynous with the pistillate phase (anthers undehisced, Figure 1A) followed by the hermaphroditic phase (anthers dehisced, Figure 1B). The flowers remain open at night; in contrast flowers of congeners having rotate corollas close at night (Mione, 1992). Although self-compatible, flowers of *J. weigendiana* are not autogamous. On plants grown for study nearly no fruit was set without manual pollination, and after manual self-pollination fruits developed and ripened in seven weeks.

In the visible spectrum the nectar of *J. weigendiana* is orange when flowers first open and subsequently turns red with age. The darkening of nectar within flowers as they age has been reported in the Lamiaceae (Zhang et al., 2012) and in *J. calliantha* (Plourd & Mione, 2016). The nectar of *J. weigendiana* absorbs ultraviolet, violet, blue and green wavelengths (Figure 3). Colored nectar that is UV-absorptive has previously been reported (Zhang et al., 2012). However, this is the first report of colored, UV-absorptive nectar for the Solanaceae. While taking into consideration that UV light is not more obvious to pollinators than other bands that nonhuman animals see (Kevan et al., 2001), it is possible that the contrast between the relatively UV-reflective corolla and the UV-absorptive nectar and nectar guides (Figure 2A) enhances the foraging signal (Thorp et al., 1975; Frohlich, 1976). Nectar is

	Ultraviolet-Visible Spectrum	
41.1		
10 5 7		
r 10	\frown	
11.24		



Figure 3. Spectrophotometric analysis of floral nectar from the flower of a cultivated plant of *Jaltomata weigendiana*.

produced by flowers in both the pistillate (Figure 1A) and hermaphroditic phases (Figure 1B). J. quipuscoae has a nectar absorbance spectrum (Mione, unpublished) that is nearly identical to that shown for J. weigendiana (Figure 3). These two species are the first to have been examined for UV absorbance; it seems likely that most or all of the Jaltomata species having red nectar (illustrated and shown in photographs by Leiva et al., 2015) will show a similar absorbance spectrum.

At least some insects (Chittka et al., 1994), bats (Winter et al., 2003), and hummingbirds (Goldsmith, 1980; Jacobs, 1992; Tovée, 1995) see ultraviolet wavelengths. Although we have not observed pollinators visiting J. weigendiana, the pollinators of a few other Jaltomata species have been recorded. Bees have been seen visiting Jaltomata spp. that have rotate or short-tubular corollas, all lacking red nectar (J. procumbens and J. repandidentata in Mexico and Costa Rica [Eickwort, 1967; Williams, 1985], and J. athahuallpae and J. diversa in Peru [Mione & Leiva G., unpublished]). Hummingbirds have been photographed visiting the long-tubular flowers (lacking red nectar) of J. viridiflora in Ecuador and the campanulate flowers (having red nectar) of J. calliantha in Peru (Leiva G. & Mione, unpublished). The corolla of J. weigendiana is campanulate and green with red nectar, and the red coloration and UV contrast (including that created by the nectar guides) may be foraging signals for hummingbirds. The red coloration may also attract insect pollinators given that there are insects with "specialised red receptors" and red is "not invisible to insects that lack a specific red receptor," (Kevan et al., 2001, p. 2577). In flowers of plants of J. weigendiana grown for study, nectar volume ranged from 7 to 57 µl (mean 28) and estimates of sugar concentration ranged from 9 to 24 % (mean 15). These sugar concentrations are similar to those reported for flowers visited by hummingbirds, hawkmoths, butterflies and bats (Pyke & Waser, 1981).

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J. alviteziana S. Leiva	J. estilopilosa S. Leiva & Mione	<i>J. procumbens</i> (Cav.) J. L. Gentry
J. athahuallpae S. Leiva & Mione	<i>J. herrerae</i> (C. V. Morton) Mione	<i>J. quipuscoae</i> Mione & S. Leiva
J. calliantha S. Leiva & Mione	J. leivae Mione	<i>J. repandidentata</i> (Dunal) Hunz.
<i>J. dendroidea</i> S. Leiva & Mione	J. neei Mione & S. Leiva	<i>J. viridiflora</i> (Humb., Bonpl. & Kunth) M. Nee & Mione
I diversa (I E Machr)	I nangoi Mione & S. Leiva	L wainandiana Mione & S

Appendix 1. Jaltomata species, with authorities, mentioned in the text and Table 1.

Minne	Tairro
Mione	Leiva